BREVIORA

STUPENDEMYS GEOGRAPHICUS, THE WORLD'S LARGEST TURTLE

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ABSTRACT: *Stupendemys geographicus,* a gigantic fossil pelomedusid turtle from the late Tertiary (Huayquerian) Urumaco Formation of northern Venezuela is described. *Stupendemys* was evidently a highly aquatic form. Whether it was a fresh water or marine turtle, however, cannot be determined with certainty on the present evidence. One or perhaps even both pairs of limbs may have been modified into flippers, and the head may not have been fully retractable in the usual pleurodiran manner. Comparisons with records of other enormous chelonians reveal that the carapace of *Stupendemys* is larger than that of any other turtle, fossil or recent.

INTRODUCTION

Paleontologists are occasionally fortunate enough to make totally unexpected discoveries. Such was the case during the summer of 1972, when a Harvard paleontological expedition working in late Tertiary deposits of northern Venezuela unearthed the remains of several huge fossil turtles. These certainly attained greater size than any other extinct chelonians yet known; they also appear to be larger than any living ones and hence the largest turtles that ever existed. The purpose of this paper is to describe these gargantuan creatures.

The following abbreviations are used:

AMNH: American Museum of Natural History, herpetological collections

MCNC: Museo de Ciencias Naturales, Caracas

MCZ: Museum of Comparative Zoology: (H), herpetological collections; (P), paleontological collections

PU: Geology Museum, Princeton University

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SYSTEMATICS

Order   Testudines
Suborder   Pleurodira
Family   Pelomedusidae

Stupendemys[1] gen. nov.

Plate 1 and Figures 1–3, 5, 6, and 9

Type species. *S. geographicus*[1] sp. nov.

Distribution. Huayquerian, Venezuela

Diagnosis. Shell gigantic; carapace depressed, with irregular nodular contours on external surface and deep median notch at front; anterior border of nuchal bone thickened and moderately to strongly upturned; posterior peripheral bones moderately scalloped along margins; neurals arranged in uninterrupted sequence, numbers two through six hexagonal, the seventh pentagonal. Mesoplastra hexagonal to subcircular, largely confined to bridge; lateral ends of pectoral-abdominal scute sulci terminating just anterior to axial notches of shell.

Cervical vertebrae (probably seventh and eighth) with saddle-shaped articulations; neural arches relatively high in relation to anteroposterior lengths of centra; angle of neural arch of presumed eighth cervical with horizontal plane greater than in any other pelomedusid; articular facets of postzygapophyses of both cervicals forming acute angle of less than ninety degrees with respect to each other; prezygapophyses of presumed eighth cervical directed more perpendicularly than in other pelomedusids; thin, bladelike spine on anterior face of eighth neural arch; no ventral keel on eighth centrum.

Angle of divergence between two ventral processes of scapulocoracoid roughly ninety degrees; ventromedial process of scapula dorsoventrally flattened; coracoid greatly thickened along medial edge; glenoid socket facing forward rather than laterally.

Humerus squat, massive, lacking ectepicondylar groove of foramen; deep bicipital fossa between radial and ulnar articular facets on ventral surface; prominent ridge traversing ventral surface of shaft from ulnar process to distal end, terminating

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[1]The generic name alludes to the astonishing size of this turtle, and the species is named in honor of the National Geographic Society in recognition of its generous support of my research on turtles.

just above radial condyle; ulnar condyle broadest at anterior end; ulnar and radial condyles facing somewhat more ventrally than in other pelomedusids; entepicondyle and supinator process strongly developed, resulting in distal expansion of humerus almost as great as that of proximal end; shaft triangular in cross-section rather than circular.

Femur squat, massive, greatly flattened dorsoventrally; breadth of tibial condyle approximately one-third total length of bone.

Stupendemys geographicus sp. nov.

Type. MCNC 244, medial portion of the carapace with associated left femur, fragments of a scapulocoracoid and a cervical vertebra, probably the eighth.

Hypodigm. The type, and MCZ(P) 4376, much of the carapace, fragments of the plastron, a cervical vertebra (probably the seventh), both scapulocoracoids and a caudal vertebra; MCNC 245, a plastron lacking the epiplastra and entoplastron, two nearly complete pleurals, several peripherals, and one neural, all from the same individual; MCZ(P) 4377, a cervical, probably the eighth; and MCZ(P) 4378, a left humerus.

Horizon and localities. "Capa de huesos" (also known as "Capa de tortugas"), upper member of the Urumaco Formation, Huayquerian (which is probably of Pliocene age; see, for example, Simpson, 1974: 5).

Outcrops of the Urumaco Formation are restricted to a relatively small area in the northwestern part of the state of Falcón, centering around the now-abandoned El Mamón oil field (lat. 11°13'N, long. 70°16'W), just north of the town of Urumaco. The type was found immediately west of Quebrado Tio Gregorio, near its mouth. Other specimens were found as follows: MCZ(P) 4376 — one-half km north of Quebrado Picacho and 50 m east of the Chiguaje fault; MCZ(P) 4377 — three and one-half km north 30° west of El Picacho on the up side of the Chiguaje fault; MCZ(P) 4378 — as for the previous specimen, but about 15 m higher in the section; MCNC 245 — three-quarters km north of Kilometer 153 on the oil pipeline running from Punta Gorda to the Paraguaná Peninsula (same locality as MCNC 238, a trionychid; Wood and Patterson, 1973).

Diagnosis. As for the genus.

DESCRIPTION

Shell. The most complete carapace is that of MCZ(P) 4376 (Plate 1), which lacks some of the anterior peripherals on the right side, as well as peripherals from the bridge region on both sides. Scute sulci are deeply impressed onto the external surface but, as in many giant chelonians, most of the bone sutures have become largely fused and the pattern of these cannot be traced with any degree of certainty. The carapace is low-arched in the manner typical of aquatic turtles, and its dorsal surface, rather than being smooth, is somewhat nodose. There is a strong median indentation at the anterior margin of the carapace that is unique among pelomedusids (and perhaps even among turtles in general) in having the bone of this region curled up into a thickened, collarlike structure. Posterior to the bridges, the peripheral bones have mildly scalloped margins. The sacral region of this specimen is fairly well preserved. There are four sacral ribs abutting against the attachments of the ilia onto the visceral surfaces of the eighth pair of peripherals; the distal ends of the last two of these are fused together. This is essentially the same pattern as reported by Zangerl (1948: 30–31 and pl. 4, fig. 3) for the largest living South American pelomedusid, *Podocnemis expansa.* There is a slight postero-medial overlap of the iliac scars onto the suprapygal. Whether these also extended forward onto the under surface of the seventh pair of pleurals (and if so, to what extent) is uncertain because the course of the suture between the seventh and eighth pairs of pleurals cannot be determined. Measurements of this carapace are given in Table 1.

The carapace of the type specimen (Fig. 1) differs in several respects from that of the one just described and moreover provides information about the shape and arrangement of the neural bones not revealed by the more complete specimen. Measurements of the vertebral scutes of the two carapaces (Table 1) indicate that the type was somewhat larger, roughly by five per cent. Its midline length, therefore, would have been in the neighborhood of ten to twelve centimeters longer, giving an estimated midline length of as much as 230 centimeters. The curling and thickening of bone at the anteromedian indentation is less pronounced in the type than in MCZ(P) 4376. The outlines of six neural bones can be traced on this specimen. The pattern revealed is typical for South American pelomedusids; the last neural, which I believe to be the seventh, is pentagonal

while those anterior to it (presumably the second through sixth) are hexagonal. The neurals, again typically, tend to become progressively broader in relation to their anteroposterior length toward the rear of the series (Table 2). As far as can be determined, the neurals were arranged in an uninterrupted sequence. Behind the last neural, part of the seventh and all of the eighth pair of pleurals meet in the midline.

An isolated neural bone from another specimen (MCNC 245) adds further information about the structure of the median part of the carapace. The bone is hexagonal and somewhat longer than broad (Table 2), indicating that it comes from the anterior part of the series. Because the first neural of pelomedusids is usually elongate and rectangular or oval, it seems reasonable to assume that the specimen in question is either the second or third. The bone was obviously in direct contact with neurals both to the front and rear. This reinforces the impression already given by the type carapace that the neural series was continuous, and, in fact, if the neural is actually the second rather than the third, proves the point. A notable feature of this neural is its exceptional thickness in proportion to its length and width; at various places around the periphery the bone measures 2.8, 2.6, and 2.4 centimeters dorsoventrally. In general, pelomedusid neurals tend to be proportionately much thinner. Although it is not feasible to measure the thickness of the individual neurals of the type carapace, it is possible to state that the carapacial bone does appear to be disproportionately thick, even for a turtle of such exceptional size. Perhaps the unusual thickness of the shell should be considered a diagnostic character of the taxon.

There is nothing remarkable about the carapace scute pattern of *S. geographicus*. It is virtually indistinguishable from that of any of the living South American pelomedusids which, except for minor variations, are all very similar.

No identifiable plastral remains are associated with the type specimen. However, the mesoplastra, hyoplastra, and right hypoplastron of MCZ(P) 4376 were recovered; these had been crushed down into and molded against the shallow bowl-shaped depression formed by the visceral surface of the carapace (the shell was found lying upside down) and unfortunately preserve little in the way of detail. Nevertheless, the presence of mesoplastra in conjunction with pelves that were clearly fused to the shell leaves no doubt that these gigantic turtles are pelomedusids.

The mesoplastra are relatively small, hexagonal to subcircular elements, laterally positioned and confined largely to the bridge. This is the standard configuration for all known living and fossil South American pelomedusids. On the basis of size and thickness, I have referred a fairly complete plastron and some miscellaneous carapacial fragments (MCNC 245; Fig. 2) to *Stupendemys*. Although very large by ordinary pelomedusid standards (Table 3), this plastron is relatively small in comparison to the carapaces described above. Presumably it represents a young adult. The forward portion of the anterior lobe is missing. This is regrettable because it is this part of the pelomedusid shell that is generally the most useful for taxonomic purposes. Nevertheless, some interesting characteristics are evident. The bridge is considerably longer at its base than the posterior plastral lobe (Table 3). The bone is exceptionally thick in proportion to its length and breadth. And, most notably, the lateral ends of the pectoral-abdominal scute sulci terminate just in front of the bases of the shell's axial notches, on the edges of the anterior plastral lobe. This position is in contrast to other South American fossil and recent pelomedusids in which these sulci typically meet marginal scute sulci on the forward third of the bridge, usually just in front of the anterior mesoplastral bone sutures. The plastral formula, insofar as it can be determined, is: femoral>abdominal>anal.

Axial skeleton. The three cervical vertebrae that have been recovered (MCZ[P] 4376, MCZ[P] 4377, and MCNC 244) belong to three different individuals and represent only two of the eight bones in the series. Measurements of these are given in Table 4. Because of the unique morphology of these vertebrae, it is difficult to be certain as to their positions in the series. In the cervicals of living pelomedusids, the neural arches become increasingly prominent from front to rear, that of the eighth always having the greatest height in relation to the length of the centrum (Table 4). The two morphologically identical fossil cervicals (MCZ[P] 4377 and MCNC 244) have neural spines that are, relatively, even more prominent than that of the eighth cervical in living pelomedusids, while the third (MCZ[P] 4376) has an arch only slightly less prominent (Table 4). On this basis it would seem likely that we are dealing with cervicals at the posterior end of the series, presumably the seventh (MCZ[P] 4376) and eighth (MCZ[P] 4377 and MCNC 244).

However, examination of the central articulations furnishes contradictory evidence. Cervicals four, five, and six of all living South American pelomedusids have saddle-shaped articulations, the seventh is similarly shaped anteriorly but convex posteriorly, and the eighth is concave in front and convex behind (Williams, 1950: 528, 532, 552, and fig. 11). The three known cervicals of *Stupendemys* have saddle-shaped articulations, and hence compare in this feature to the fourth through sixth cervicals of the extant South American pelomedusids, rather than to the seventh or eighth. (Undescribed fossil pelomedusid cervicals from the late Cretaceous of Brazil, which I have been able to examine through the courtesy of Dr. L. I. Price, are indistinguishable from those of living South American representatives of the family.) In living African pelomedusids, the centra of cervicals three through eight are uniformly procoelous (Williams, ibid.). Cervicals are known for only one African fossil pelomedusid (Wood, 1971), and these differ from both living African and South American forms in having articular surfaces intermediate in shape between the saddle joints of the latter and the procoelous condition of the former. No cervicals have been reported for fossil pelomedusids from continents other than Africa and South America, the only regions, together with Madagascar, where the family still survives. The cervical articulations of *Stupendemys* are therefore most closely comparable to those of its South American relatives.

Because the trend of anteroposteriorly increasing neural spine height seems to be consistent in all pelomedusids, whereas the pattern of cervical articulation varies somewhat, I am inclined to place more reliance in the former feature as a means for determining the relative position of the *Stupendemys* neck vertebrae in the cervical series. As Table 4 shows, the height/length ratio of the eighth cervical is always the greatest for any individual. Moreover, as shell size increases, the height/length ratio also increases, so that it is greater for the eighth cervical of *Podocnemis expansa* than for that of the much smaller *Pelomedusa subrufa*. Given these observations, and in view of the fact that the height/length ratios of MCZ(P) 4376 and MCNC 244 are considerably greater than those recorded for any of the Recent species, while that of MCZ(P) 4376 is about the same as the greatest ratio for the largest Recent specimen measured, it seems that the cervicals of *Stupendemys* are from the posterior part of the series, probably representing the seventh and eighth.

If the cervicals of *Stupendemys* are, in fact, the seventh and eighth, then they are unique among known pelomedusids by virtue of their saddle-shaped articulations. There are, in addition, several other features of these vertebrae that reinforce this impression. One of the most obvious is that the neural arch of the eighth cervical of *Stupendemys* makes a much less acute angle with the anteroposterior axis of the centrum than do those of the comparable cervical in other pelomedusids. (In the cervical series of Recent pelomedusids that I have examined, the neural arch of the eighth cervical always makes the greatest angle to the horizontal plane.) In posterior view, the articular facets of the postzygapophyses form an acute angle of less than ninety degrees with each other. Those of other pelomedusids are nearly horizontal to the dorsoventral axis of the vertebrae (fig. 4; see also Williams, 1950, fig. 11). Viewed laterally, the shafts of the prezygapophyses of the presumed eighth cervicals of *Stupendemys* are directed much more perpendicularly than those of other pelomedusids. Although impossible to measure precisely, the angle made with the horizontal plane in the specimens of *Stupendemys* seems to be roughly sixty to seventy degrees, whereas in others it is closer to thirty degrees (cf. figs. 3 and 4). The thin, median, bladelike spine on the anterior face of the neural arch of the presumed eighth cervical of *Stupendemys* is also unlike anything seen on comparable parts of other pelomedusid cervicals. In most pelomedusids, the ventral surfaces of the cervical centra are typically bowed upwards, sometimes quite strongly, along the anteroposterior axis. The one exception known to me is the eighth cervicals of South American representatives of *Podocnemis*. In these, a flat blade of bone projects downward from the ventral surface (Fig. 4). But in both examples of the presumed eighth cervical of *Stupendemys*, the ventral surface is neither bowed upwards nor downwards; it is, instead, flat. Unfortunately, the bottom of the presumed seventh cervical vertebra (MCZ[P] 4376) is too badly damaged to determine its original shape.

A single, small caudal vertebra was found in association with one of the shells (MCZ[P] 4376). It is poorly preserved and reveals no features of special interest.

Appendicular skeleton. Much of both scapulocoracoids have been preserved for MCZ(P) 4376, as well as fragments of one belonging to the type. It is not possible to determine with certainty the relative lengths of the three prongs making up the

shoulder girdle. The medial tips of the ventromedial portions of the scapulae are broken off. The dorsal processes of this same bone have been broken at their bases and flattened into the same plane as the other two elements. Since their basal contacts have been obliterated, it is impossible to determine how much (if any) of these processes is lacking. The coracoids, however, appear to be complete. Both the left and right ones are of essentially the same lengths in MCZ(P) 4376 and are considerably longer than what remains of the ventromedial processes of the scapula, but slightly shorter than the more complete of the two dorsal scapular processes that have been preserved (Table 5). These proportions are in accord with those of Recent pelomedusids, in which the ventromedial process of the scapula is much shorter than the dorsal one, while the coracoid is intermediate in length, generally somewhat flattened dorsoventrally, and moderately to greatly expanded towards its extremity. Despite this incompleteness a number of distinctive features are evident. The glenoid socket faces almost directly forward in *Stupendemys*, whereas in typical pelomedusids it tends to face in a lateral direction (Fig. 5). The angle at which the two ventral prongs of the scapulocoracoid diverge is considerably less acute in *Stupendemys* than in any other known pelomedusid (Fig. 5). The shoulder girdle of *Stupendemys* further differs from those of typical Recent South American pelomedusids in that the ventromedial process of the scapula is dorsoventrally flattened. In specimens of *Podocnemis dumeriliana*, *P. expansa*, and *P. unifilis* that I have examined, this bone is anteroposteriorly flattened. The medial side of the coracoid of *Stupendemys* is greatly thickened. This is not true of the coracoids in living African representatives of the family, which are uniformly thin, flat, and greatly expanded. In typical South American pelomedusids as well as in *Podocnemis madagascariensis*, the coracoid is not so expanded but is transversely arched, with the apex of the arch on the dorsal side. (The one exception of which I am aware is *Podocnemis erythrocephala* [Mittermeier and Wilson, 1974]; the coracoid of this species does not expand at all towards its tip but remains uniformly oval along its entire length [e.g., MCZ(H) 10096].) The coracoid of *Stupendemys* may have been similarly arched, if the dorsoventral crushing of this element is taken into account. The thickness of bone along its medial edge, however, still seems to set it apart from the other South American forms. The dorsal scapular process in *Stupendemys* appears somewhat flattened,

whereas in Recent pelomedusids it is more oval in cross-section. This flatness, however, may result from crushing in the horizontal plane; because of my uncertainty about this feature I have refrained from listing it as a diagnostic character.

A nearly complete left humerus (MCZ[P] 4378) is all that is known of the forelimb. This specimen is of great interest in that it is totally unlike the humerus of any other known chelonian — let alone pelomedusid — living or fossil. The head as well as the terminal portions of the radial and ulnar processes are missing, but otherwise the bone is complete (Fig. 6). This humerus is extraordinarily massive, with distal and proximal ends both markedly expanded, the latter slightly more so than the former (see Table 5 for measurements). The curvature of the shaft does not appear to differ appreciably from that of living pelomedusids. There is no trace of an ectepicondylar groove or foramen on the dorsal surface, a feature present in all other pelomedusids (and, indeed, chelonians in general). Between the radial and ulnar processes, on the ventral side, is a very deep, semicircular depression, the bicipital fossa. This is more prominent than in the fossil pelomedusid *Bothremys barberi* (Zangerl, 1948:34 and fig. 13; Gaffney and Zangerl, 1968) or *Podocnemis* but is developed to about the same extent as in *Pelomedusa* or *Pelusios*. Immediately above the articular facets on the ventral surface at the distal end of the shaft is a very deep, triangular fossa. This seems to be a natural depression rather than the result of poor preservation of the bone and has no equivalent, so far as I have been able to determine, elsewhere within the order. A thick, prominent ridge extends transversely across the ventral surface from the base of the ulnar process to a point adjacent to the radial condyle. Such ridges are absent in living pelomedusids, although less pronounced ones have been reported in fossil pelomedusids, *Bothremys* (Zangerl, 1948) and *Taphrosphys* (Gaffney, 1975; Fig. 8, this paper). Typically, the ulnar condyle in pelomedusids has a spool-shaped outline, equally expanded at both ends. The ulnar condyle of *Stupendemys*, however, is markedly broader at its anterior end than at its posterior limit. A further distinctive feature of *Stupendemys* is that the trochlea extends farther onto the ventral surface than in other pelomedusids. To either side of the trochlea, the supinator process and entepicondyle bulge outwards, the latter especially. Only in *Taphrosphys* is the distal end of the humerus expanded to such an extent (distal width over total length equals 0.47 in

Taphrosphys [Gaffney, 1975, p. 16], 0.44 in *Stupendemys*). In cross-section, midway between the ends, the shaft is triangular rather than circular or oval, as is typically the case for pelomedusids.

A left femur (Fig. 9) was found associated with the type shell. The head and terminal portions of both trochanters are missing, as well as some bone from an area at the distal end of the dorsal surface. The distal articular surfaces, however, have been largely preserved. If complete, the femur would have been of essentially the same length as the only known humerus (Table 5). Like the humerus, the femur of *Stupendemys* is massive. Its shaft is oval in cross-section and greatly flattened dorsoventrally. The shaft of *Podocnemis expansa* is also oval in coss-section but is instead flattened antero-posteriorly. As for the humerus of *Stupendemys*, the curvature of its femur does not seem to differ significantly from that of living pelomedusids. The distal end of the shaft is markedly expanded, much more so than in *Podocnemis expansa* (distal width over total length equals 0.47 in *Stupendemys*, 0.29 in *P. expansa* [MCZ(H) 4469]).

DISCUSSION

Stupendemys has many very unusual anatomical features. No modern chelonian is at all comparable to it, nor does it closely resemble any of the better known fossil turtles.

Its systematic position, at least, is clear: it is an aberrant member of the Pelomedusidae. This is conclusively demonstrated by several characters: 1) the presence of mesoplastra; 2) fusion of the pelvis to carapace and plastron; and 3) shape of the cervical articulations.

It is when one strives to understand *Stupendemys* as a living animal that difficulties arise. In the following pages I attempt a functional analysis of the known parts of the skeleton, searching for clues to behavior and habitat.

The relatively low-arched carapace of *Stupendemys* indicates that it was almost certainly a highly aquatic form, as are all living pelomedusids and most fossil ones. Pelomedusids (not yet formally described) from two different African fossil localities, one of Oligocene and the other of Miocene age, are the only terrestrial members of the family yet known (Wood, 1971). These forms had extremely high-domed shells, superficially very tortoiselike in appearance. Conversely, the only strictly terres-

trial, flat-shelled turtle is the exotic pancake tortoise of East Africa, *Malacochersus,* and its shell structure represents an adaptation to most unusual habits. Shell shape thus seems to be a nearly infallible indicator as to whether a chelonian was aquatic or terrestrial, and *Stupendemys* clearly falls into the former category.

The strong median indentation at the front end of the cara-pace is not characteristic of pelomedusids in general, but is reminiscent of the condition seen in the unrelated, big-headed turtle, *Platysternon,* of southeast Asia. *Platysternon* has a very large head in proportion to the size of its shell; consequently, individuals of this genus are not able to withdraw their heads into the shell in the typical cryptodiran manner. But the an-terior embrasure of the carapace provides a notch into which the back of the head fits when retracted to the maximum extent possible. The heavily boned dorsal roof of the skull then acts, in effect, as an anterior continuation of the carapace and evi-dently serves as a reasonably effective deterrent to predators. *Stupendemys,* too, may have had a proportionately large, heavily armored skull which did not have to be swung under the cara-pace for protection in the usual pleurodiran fashion, but instead was simply lodged against its anterior border when danger was imminent.

I cannot readily account for the significance of the thickened, curled-up bone at the anterior margin of the carapace. It might represent a variably-expressed secondary sexual character if the two carapaces in the available sample represent opposite genders. It has, so far as I am aware, no structural equivalent elsewhere within the order.

South American pelomedusids are the only chelonians having saddle joints on the articular surfaces of their cervical centra (Williams, 1950, appendix 1). But, as pointed out (p. 8), the cervical vertebrae of *Stupendemys,* although possessing the characteristic saddle joints, are in detail very different from those of any pelomedusid known from that continent or else-where. This fact supports the supposition that neck retraction in the genus was fundamentally different from that of other pleurodires. But if, as suggested above, *Stupendemys* was com-parable to *Platysternon* in its ability to retract its skull only partially, then the similarities in behavior were not paralleled by structural resemblances of even the most superficial kind. The articular surfaces of the fifth through eighth cervical **centra** in *Platysternon* are generally doubled, the centra themselves are

very broad and flat, the neural arches lack spines, and so on. In sum, while it is clear that the cervicals of *Stupendemys* are markedly different from those of any other known turtle, the significance of these differences is not readily apparent.

Regrettably, the relative sizes of the humerus and femur in *Stupendemys* cannot be determined with any degree of certainty. This is unfortunate because, for turtles in general, the proportions of the fore and hind limbs are good indicators of the customary mode of progression. Pelomedusids and most aquatic cryptodires rely primarily on their hand limbs for propulsion while swimming, hence their femora are larger than their humeri. But in tortoises and marine turtles, the opposite is true. Thus, for example, if it were possible to establish that the humerus of *Stupendemys* was larger than its femur, this might be taken as reasonably good presumptive evidence that this peculiar pelomedusid swam in a different way from all other pelomedusids — perhaps even with flipperlike appendages, as in the modern marine turtles. But direct comparisons between the humerus and femur of a single specimen of *Stupendemys* are impossible. Moreover, the only known humerus of *Stupendemys* was an isolated find, which therefore cannot be tied to shell size, so that even indirect comparisons (in which limb size is related to shell length) cannot readily be made.

Normally, limb structure is also a good index to the locomotory capabilities of turtles. The highly modified, flippered forelimbs of marine cryptodires have a humerus that tends to be broad, flat, and relatively straight-shafted. In aquatic (or largely aquatic) forms, such as the pleurodires and emydines, it is much more gracile, ordinarily more or less circular in cross-section, and with a moderate curvature of the shaft. Tortoise humeri are stout and often have a strongly bowed shaft. The humerus of *Stupendemys* does not fall satisfactorily into any of these broad categories. It is considerably more massive even than that of a tortoise, fairly straight in the shaft, but more circular than flat in cross-section. The heavy ridge across the ventral surface of the shaft almost surely provided an increased area for the attachment of hypertrophied antebrachial musculature. Such muscles would only be required if the distal extremity of the forelimb were for some reason disproportionately large, as in marine turtles. While admittedly tenuous, this line of reasoning leads me to suspect that the forelimb of *Stupendemys* was modified into a paddle, a structure highly efficient for swimming but ill adapted to a terrestrial existence of any

sort. Given the absence of direct fossil evidence, however, this can only be a very tentative suggestion.

The humerus of the fossil pelomedusid *Taphrosphys* (Fig. 8; Gaffney, 1975, fig. 12) appears to be intermediate in structure between that of *Stupendemys* and those of typical representatives of the family. Unfortunately, the humerus is the only part of the forelimb of *Taphrosphys* so far known, so that this taxon provides no further insight into the structure and function of the *Stupendemys* forelimb.

Forms intermediate in femoral structure between *Stupendemys* and the typical pelomedusids (or turtles in general, for that matter) do not exist. Had the femur not been found in association with pelomedusid shell remains, its familial allocation would have been impossible. Differences between the femur of *Stupendemys* and that of a representative pelomedusid (*Podocnemis expansa*) have already been enumerated (p. 11). The strongly projecting trochanters, broad intertrochanteric fossa and flattened shaft of *Stupendemys* distinguish it readily from both marine cryptodires and tortoises, while the massiveness of the bone and the broad, flat shaft together differentiate it from that of the other aquatic forms. In these characters, in fact, together with the relative straightness of the shaft, the femur of *Stupendemys* is more like the forelimb of marine turtles than anything else. For this reason it is tempting to speculate that the hind limbs of *Stupendemys* may have been modified into paddling flippers as large as those possibly present on its forelimb.

In sum, the available anatomical evidence demonstrates that *Stupendemys* was an aquatic form. In all likelihood, one or perhaps even both pairs of limbs were modified as flippers. The very size of its shell suggests that *Stupendemys* must have inhabited large, permanent bodies of water which it probably left only to lay eggs. Among living aquatic turtles in general, the larger the species, the less likely it is to come out of the water except for nesting. Size alone probably prevented *Stupendemys* from basking along shores. Flippers, if it had them, would have made such an undertaking even more awkward. I suspect that *Stupendemys* was largely if not entirely herbivorous, again simply because of its size; all of the largest living turtles — land tortoises as well as the marine forms — are totally (or nearly totally) herbivorous.

Geological evidence, although often helpful in attempting to determine the habitat of a fossil, is, in the present case, equivocal. A variety of different facies are represented in the upper

member of the Urumaco Formation, including near-shore marine, brackish, and fresh water deposits. Some of these fresh water facies consist largely of platy concretion zones, which are probably best interpreted as representing small ephemeral ponds. Root casts and locally abundant leaf impressions are also characteristic of these deposits. Mammalian remains (especially very large rodents) tend to be more abundant here, as are certain of the reptiles (e.g., *Chelus,* nettosuchids). Other fresh water deposits probably represent stream channels and, in some cases, swampy areas (as evidenced by localized accumulations of vegetable debris). In general, the vertebrate-bearing sediments were evidently laid down in a coastal area over which the position of the shoreline fluctuated back and forth repeatedly. *Stupendemys* could thus have been a marine form that washed up on a barrier beach or was stranded in the lagoonal waters behind one. Or it may have been a fresh water form carried to the delta of a large river system and buried there. Since the associated fossil fauna has strong Amazonian affinities and is deficient in typical marine components, the latter possibility seems strong. But all of the largest known aquatic turtles, both living and fossil, are marine forms. This fact, coupled with the fairly convincing presumptive evidence that a number of other fossil pelomedusids were marine forms,[1] prevents categorical rejection of the idea that *Stupendemys* may have been a marine turtle.

The largest of the living pelomedusids (all of which are fresh water forms) is *Podocnemis expansa,* which has a wide distribution throughout much of the Amazon and Orinoco River basins of South America. This species is sexually dimorphic, the females growing to much larger adult size than males (Ojasti, 1971). In a large sample taken from the Orinoco River over a period of several years, the maximum carapace length for a male was 51 centimeters whereas that for a female was 81 centimeters (J. Ojasti, personal communication). The largest shell of this species yet reported is 82 centimeters long (Williams, 1954: 293). Presumably this record is of a female, although the sex of this particular specimen was not indicated. With the excep-

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[1] Included among these are several species of *Taphrosphys* (Schmidt, 1931; Gaffney, 1975; Wood, 1975), *Bothremys* (Zangerl, 1948; Gaffney and Zangerl, 1968), and a generically indeterminate form from Puerto Rico (Wood, 1972). All of these were found in near-shore marine sediments, generally under circumstances such that they cannot reasonably be regarded as exotic elements washed in from a nonmarine environment.

tion of *Stupendemys,* no known fossil pelomedusids exceed *Podocnemis expansa* in size, nor do representatives of the only other known family of side-necked (pleurodiran) turtles, the Chelidae, ever approach *P. expansa* in size. Thus *Stupendemys* is by far the largest pleurodire, living or fossil, yet known.

A few species of living fresh water cryptodiran turtles attain greater carapace lengths than *P. expansa,* but none are reliably known to approach the size of *Stupendemys.* A length of nearly 130 centimeters has been recorded for the carapace of the Asiatic trionychid *Pelochelys bibroni* (Pope, 1935). Another Asiatic soft-shelled turtle, *Chitra indica,* is generally believed to have a maximum carapace length of approximately 90 centimeters. One unsubstantiated report indicates that *Chitra* may occasionally reach a carapace length of roughly 180 centimeters (Pritchard, 1967:211). No other living or fossil fresh water cryptodires as large as either of these recent trionychids are known.

Some other fossil cryptodiran turtles of enormous size have been described, but none of these had shells as large as those of *Stupendemys. Archelon ischyros,* from the Cretaceous of North America, is the largest of the fossil marine turtles; its straight-line carapace length is 193 centimeters (Wieland, 1909). When first described, *Geochelone atlas* (originally and rather appropriately named *Colossochelys*) was believed to reach twelve feet in carapace length (Falconer and Cautley, 1844). This estimate was based on composite reconstructions of fragmentary material and has subsequently been modified to a maximum of six feet (roughly 180 cm; see Lydekker, 1889, and Auffenberg, 1974: 173). None of the specimens that have since been referred to *G. atlas,* which is now known from the Pleistocene of India, Burma, Java, Celebes, and Timor (Hooijer, 1971; Auffenberg, ibid.), appears to have reached or exceeded this length. One or more species of *Geochelone* from the Pleistocene of Florida and Texas may also have attained similarly gigantic dimensions (W. Auffenberg, personal communication). However, no tortoises — living or fossil — ever seem to have grown any larger.

In fact, of all known turtles, only the anatomically peculiar marine turtle *Dermochelys coriacea* may rival *Stupendemys* in size. *Dermochelys,* commonly referred to as the leatherback, is reputedly the largest of all turtles, living or fossil. Adults consistently attain carapace lengths of over 150 centimeters (Pritchard, 1971). In the only large series of measurements ever made, involving 1500 mature female specimens encountered laying eggs

on the beaches of French Guiana over several field seasons, the maximum length recorded was 180 centimeters (three individuals; P. C. H. Pritchard, personal communication). Larger specimens have occasionally been reported, up to a supposed length of 3.35 meters, but these are unusual and suspect because they are probably based on estimates rather than actual measurements (Carr, 1952:446), and, as Brongersma (1968:38–39) has noted, estimates of the sizes of free-swinging marine creatures generally tend to be greatly exaggerated. Thus, there do not seem to be any reliable records of leatherbacks that equal or exceed *Stupendemys* in carapace length. On the average, certainly, carapace lengths of *Dermochelys* are significantly shorter than those of *Stupendemys*. Moreover, if the known specimens are typical representatives of *Stupendemys*, then adult populations evidently tended to be significantly larger than those of *Dermochelys* are today. In sum, it is clear that *Stupendemys* is unquestionably larger than any other previously described fossil turtle and it also appears to be larger than any living species. *Stupendemys*, therefore, is the largest turtle that ever lived.

TABLE 1

Measurements (in cm) for carapaces of *Stupendemys geographicus*. Dimensions are given as straight-line distances rather than over the curvatures of the shells.

		MCNC 244	MCZ(P) 4376
midline length (as preserved)		184	218
total midline length		approx. 230	218
maximum width (estimated)		190-195	185
maximum parasagittal length		250	235
first vertebral	length	37.1	34.5
	width	approx. 26	approx. 24
second vertebral	length	33.5	34.0
	width	36.4	32.7
third vertebral	length	33.3	32.4
	width	39.3	34.4
fourth vertebral	length	39.3	37.8
	width	approx. 34	28.1
fifth vertebral	length	—	52.4
	width	—	51.7

TABLE 2

Neural bone measurements (in cm) for specimens of *Stupendemys geographicus.*

Specimen No.	Neural No.	Midline Length	Maximum Width	Width/ Length
MCNC 244	3	16.3	14.8	.91
”	4	16.6	19.2	1.16
”	5	15.5	18.0	1.16
”	6	11.7	19.0	1.62
”	7	11.4	14.9	1.30
MCNC 245	2 or 3	7.7	6.5	.84

TABLE 3

Measurements (in cm) of the plastron (MCNC 245) referred to *Stupendemys geographicus.*

midline length (as preserved)		57.2
total midline length (estimated)		76
width at axial notch		34.0
width at inguinal notch		35.3
anteroposterior length of bridge	{ left side	35.2
	} right side	36.2
midline length of posterior lobe		21.0
parasagittal length of posterior lobe	{ left side	25.2
(to tips of xiphiplastra)	} right side	25.5

TABLE 4

Measurements (in cm) of the cervical vertebrae of *Stupendemys* compared with those of adult representatives of each of the three living pelomedusid genera. (MCZ [H]4469, *Podocnemis expansa;* AMNH 10065, *Pelusios subniger;* MCZ[H]146146, *Pelomedusa subrufa*) .

Specimen No.	Midline Carapace Length	No. in Cervical Series	Midline Length of Centrum	Height of Neural Arch Spine above Base of Posterior End of Centrum	Height/ Length
MCZ(P)4376	218	7(?)	9.0	13.4[1]	1.49
MCZ(P)4377	?	8(?)	9.0	15.1	1.67
MCNG 244	230	8(?)	10.8	18.7	1.73
MCZ(H)4469	72.2	5	3.1	2.8	0.90
"	"	6	3.5	3.3	0.94
"	"	7	3.6	4.1	1.14
"	"	8	2.7	3.9	1.44
AMNH 10065	24.2	5	1.3	1.1	0.85
"	"	6	1.3	1.2	0.92
"	"	7	1.6	1.5	0.94
"	"	8	1.5	1.5	1.00
MCZ(H)146146	12.8	5	1.0	0.6	0.60
"	"	6	1.0	0.7	0.70
"	"	7	1.1	0.8	0.73
"	"	8	1.0	0.9	0.90

[1]The bottom of the posterior end of this centrum is somewhat damaged so that a precise measurement is impossible; the figure recorded here is an estimate.

TABLE 5

Measurements (in cm) of the known appendicular skeletal elements of *Stupendemys geographicus*.

SCAPULOCORACOID (MCZ[P]4376)

lengths (as preserved) of dorsal processes of scapulae	left:	36.2
	right:	39.7
lengths (as preserved, along anterior edge, starting from lateral side of glenoid fossa) of ventro-medial prongs of scapulae	left:	25.3
	right:	26.9
lengths of coracoids	left:	37.0
	right:	36.9

HUMERUS (MCZ[P]4378)

length (as preserved)	31.0
estimated total length	34
maximum width of proximal expansion (as preserved)	18.0
maximum width of distal expansion	15.0
dorsoventral width at middle of shaft	8.3
anteroposterior width at middle of shaft	6.4
combined widths of ulnar and radial condyles on ventral surface	10.1

FEMUR (MCNC 244)

length (as preserved)	29.5
estimated total length	33-34
maximum width of distal expansion	15.7
dorsoventral width at middle of shaft	6.5
anteroposterior width at middle of shaft	8.0

Plate 1. The carapace of *Stupendemys geographicus* (MCZ[P]4376), in dorsal view. Note especially the strongly curled bone at the base of the antero-median indentation. Midline length of this specimen is 218 cm. Peripheral bones in the region of the bridge on both sides, some of the more anterior peripherals on the right, and the lateral ends of some of the pleurals have been restored.
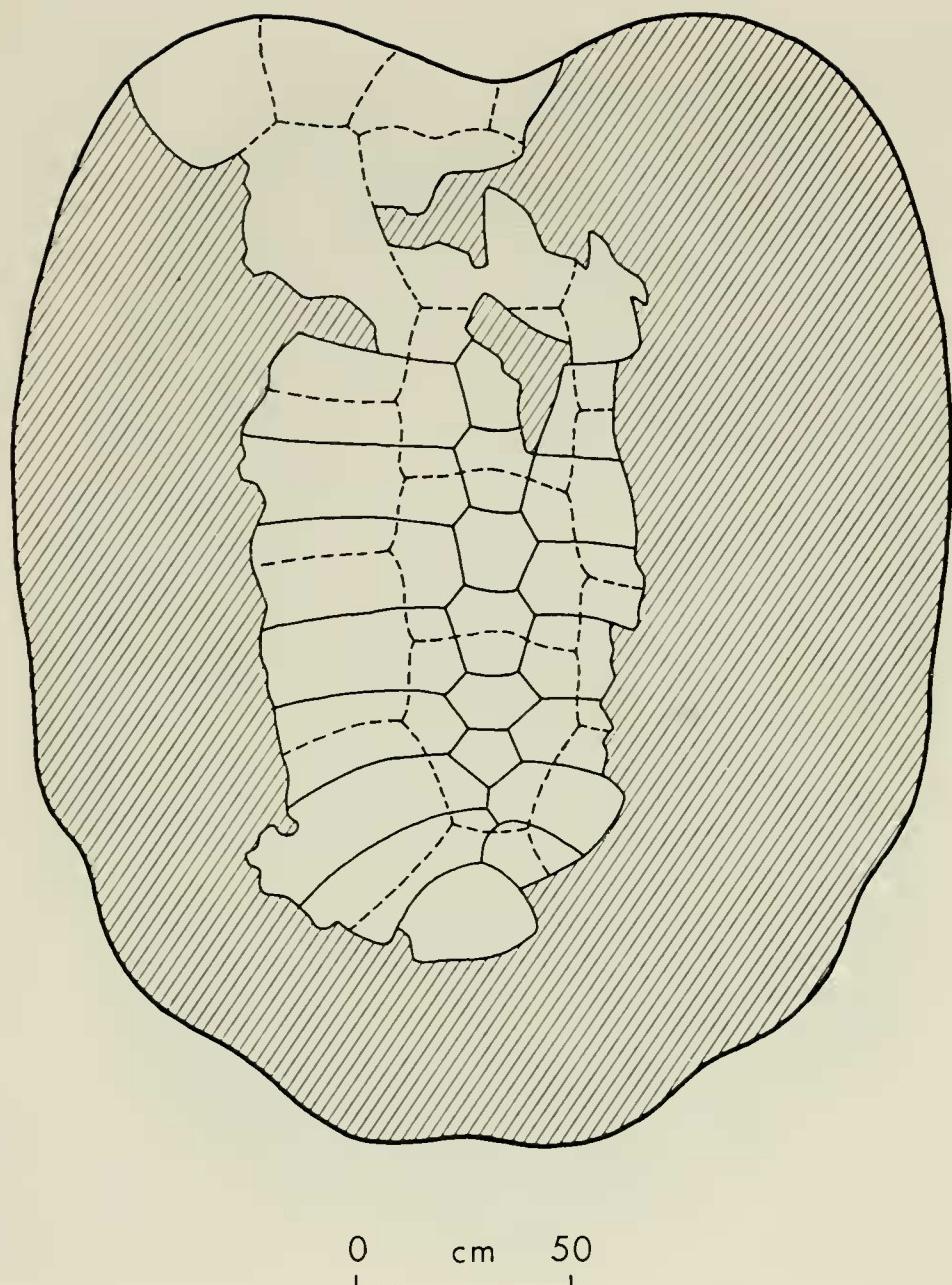
Figure 1. Carapace of the type of *Stupendemys geographicus* (MCNC 244) showing the shapes and positions of the second through seventh neural bones.
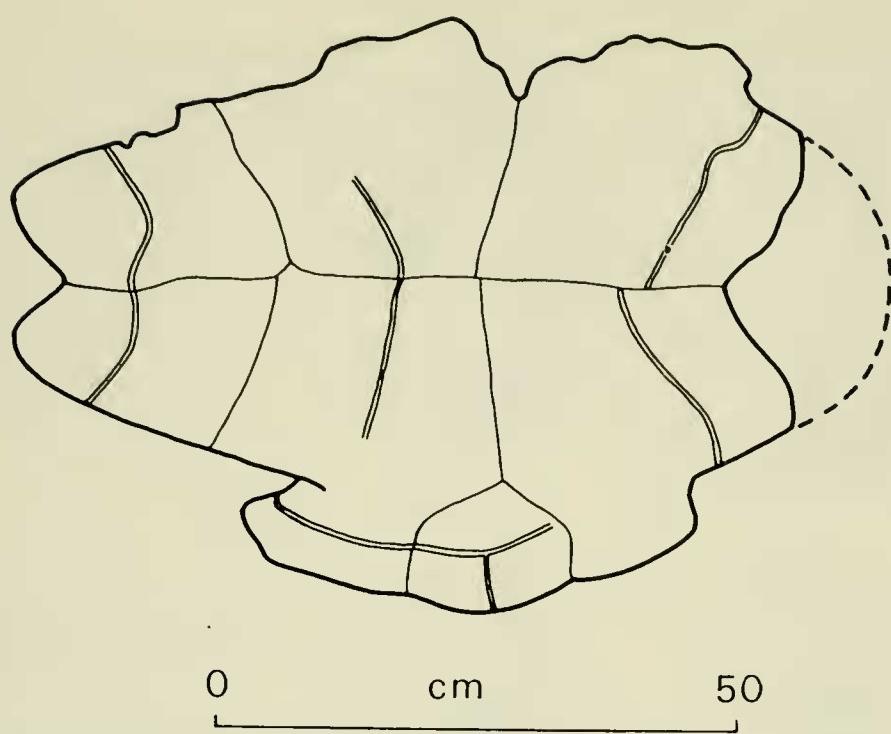
Figure 2. Sketch of a plastron (MCNC 245) referred to *Stupendemys geographicus,* showing the unusual position of the pectoral-abdominal scute sulcus. The full extent of the abdominal-femoral scute sulci cannot be traced.
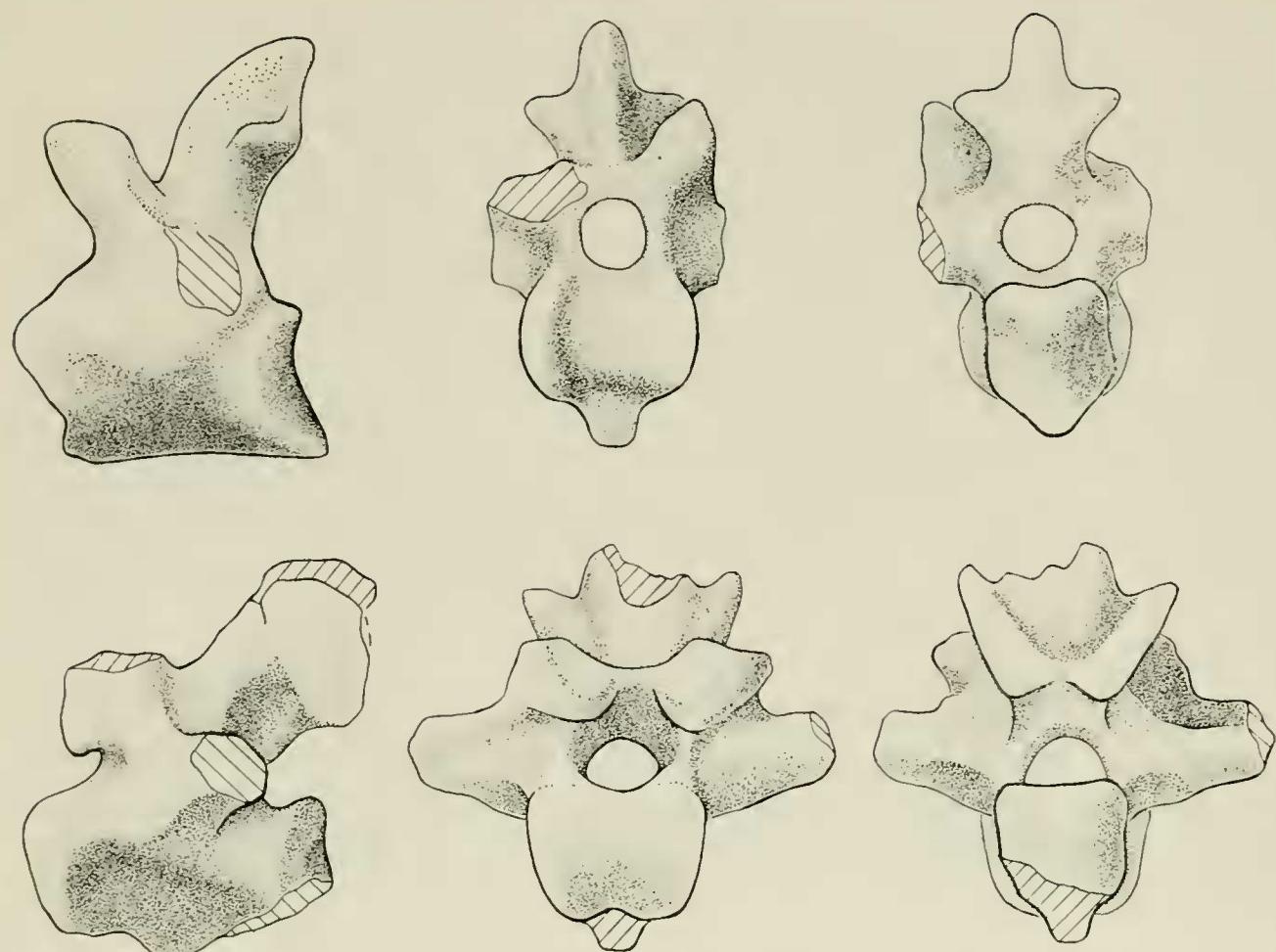
Figure 3. The seventh (bottom; MCZ[P]4376) and eighth (top; a composite based on MCNC 244 and MCZ[P]4377) cervical vertebrae of *Stupendemys geographicus* in left lateral (left), anterior (center), and posterior (right) views.
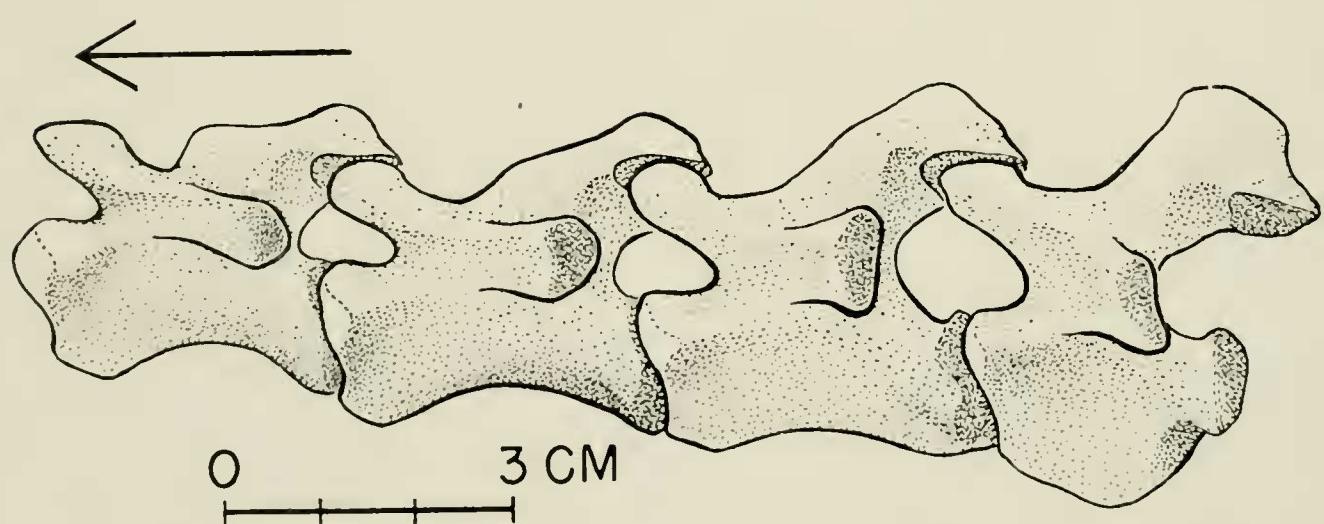
Figure 4. The fifth through eighth cervical vertebrae of *Podocnemis expansa* (MCZ[H]4469) in left lateral view. The arrow points toward the anterior end of the neck. Compare with the lateral views of Figure 3.
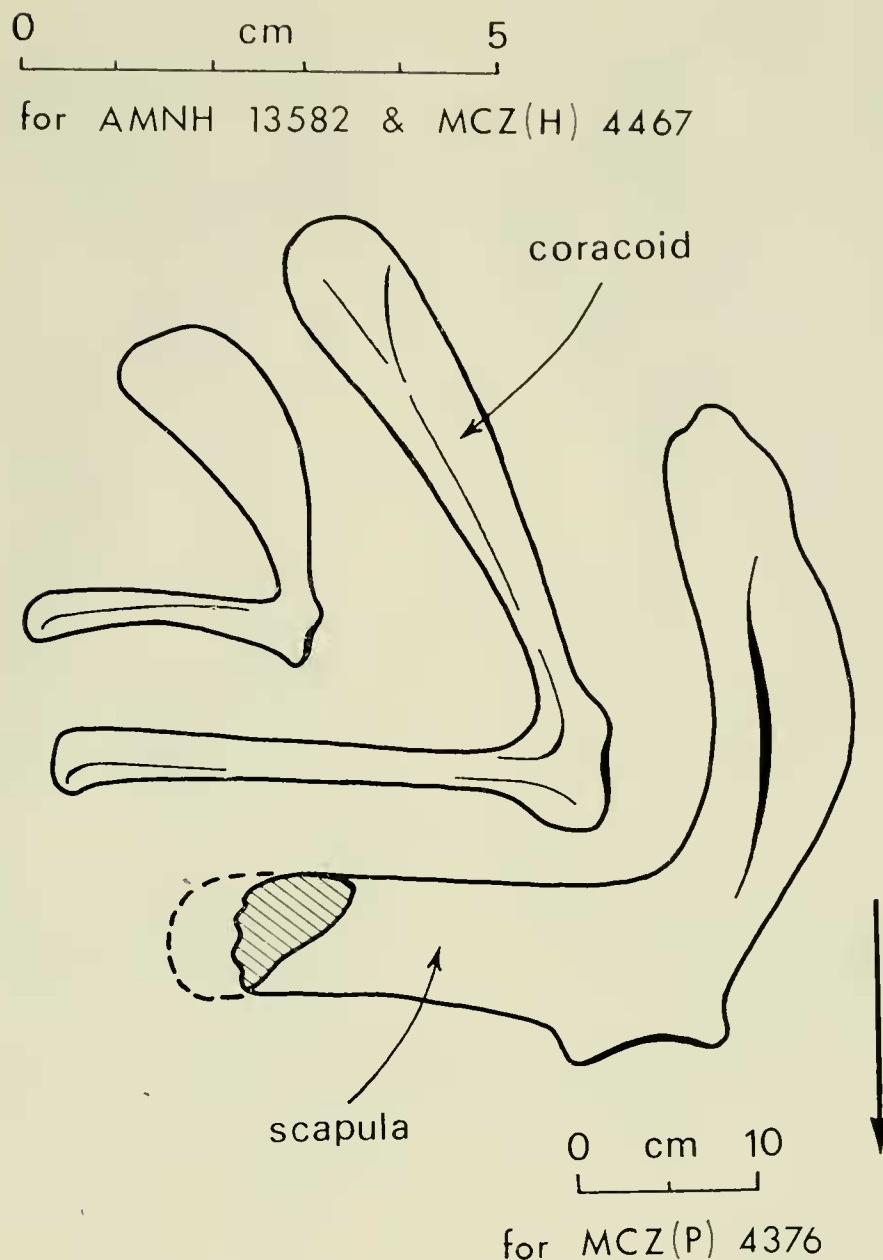
Figure 5. The ventral elements of the left scapulocoracoid of *Stupendemys geographicus* (MCZ[P]4376; bottom) juxtaposed with comparable bones of the Recent pelomedusids *Podocnemis unifilis* (MCZ[H]4467; middle) and *Pelusios castaneus* (AMNH 13582; top). The midline axis of the specimens to which they belong would be toward the left margin of the page. The arrow points anteriorly. The glenoid socket of the fossil faces forward while those of the Recent specimens are directed laterally. For clarity, the dorsal prong of the scapula and the suture between the scapula and coracoid have been omitted.
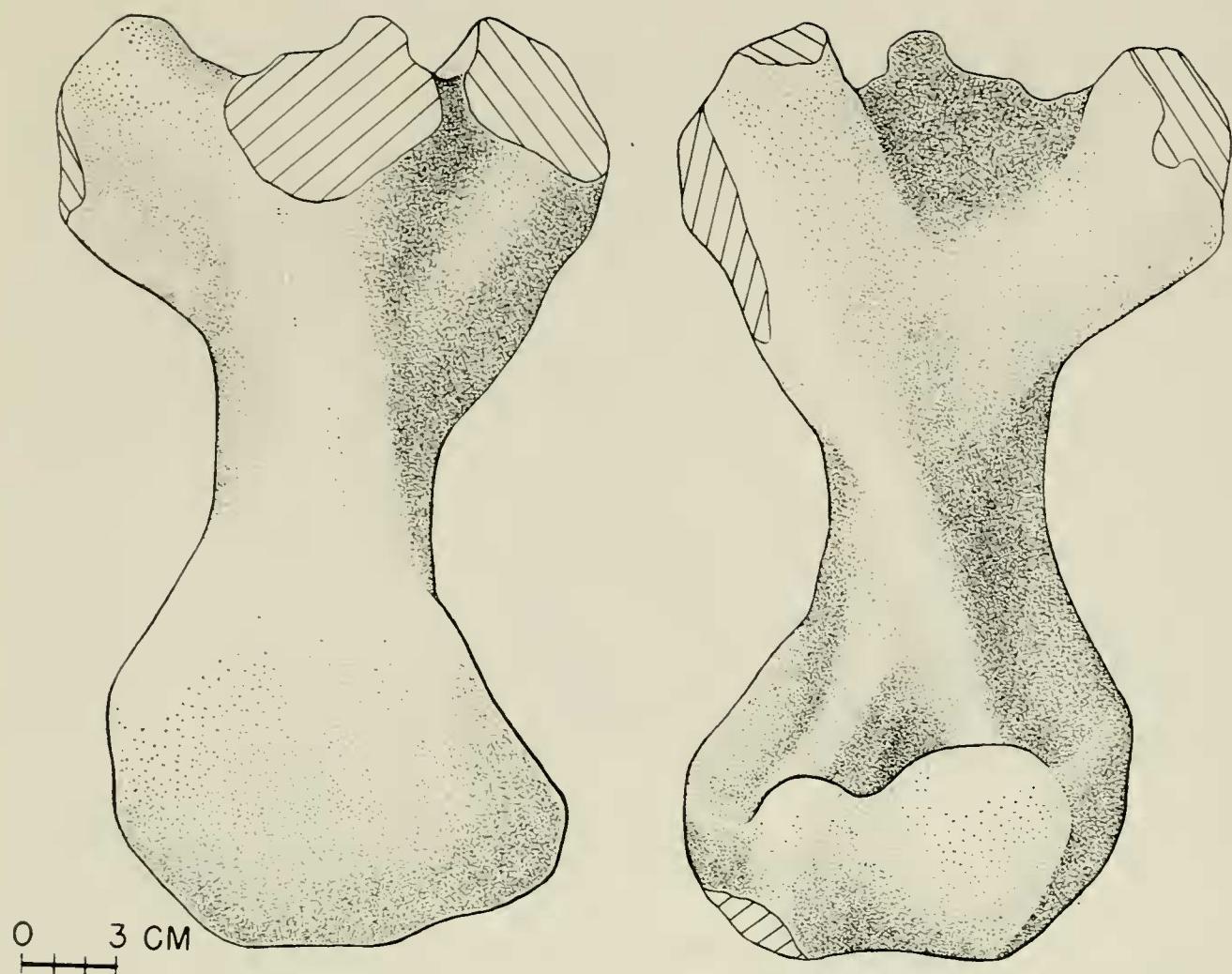
Figure 6. The left humerus of *Stupendemys geographicus* (MCZ[P]4378) in dorsal (left) and ventral (right) views.
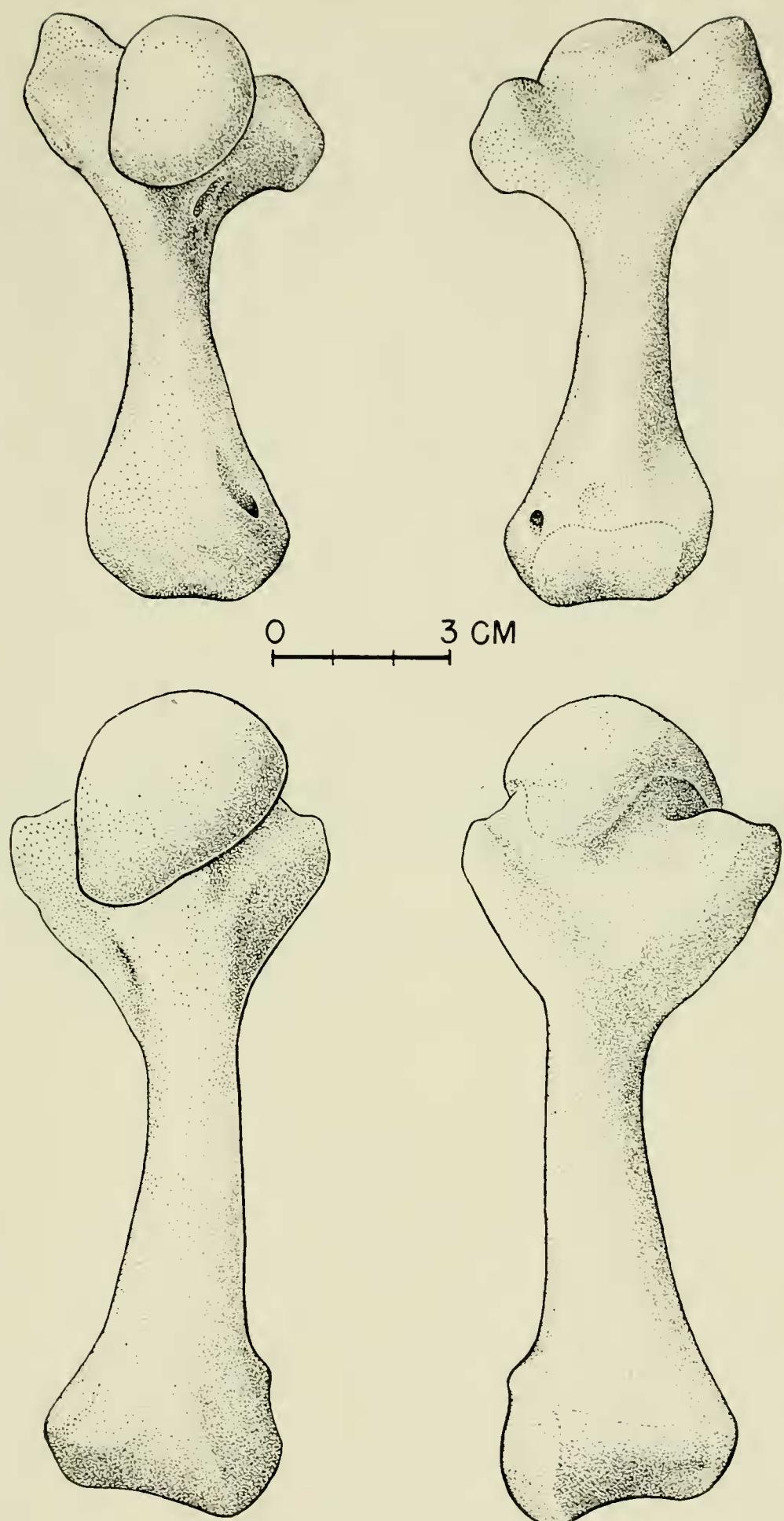
Figure 7. The left humerus (top) and left femur (bottom) of *Podocnemis expansa* (MCZ[H]4469) in dorsal (left) and ventral (right) views. Compare with Figures 6 and 9.
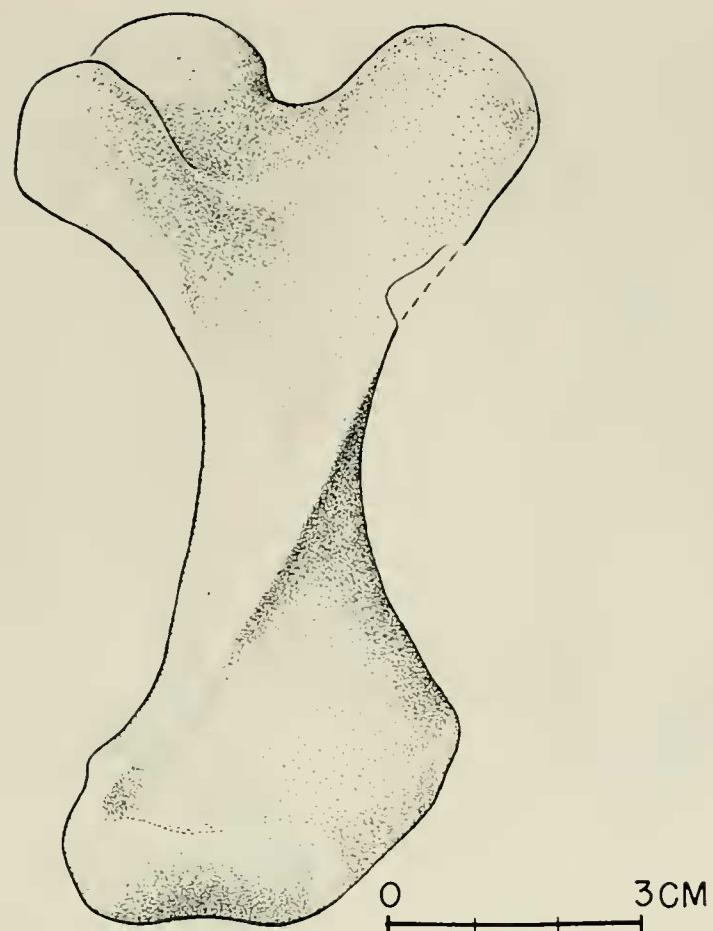
Figure 8. The right humerus of *Taphrosphys sulcatus* (PU 18707) in ventral view, showing the prominent ridge extending from the base of the ulnar process to just above the radial condyle. Compare with Figure 6.
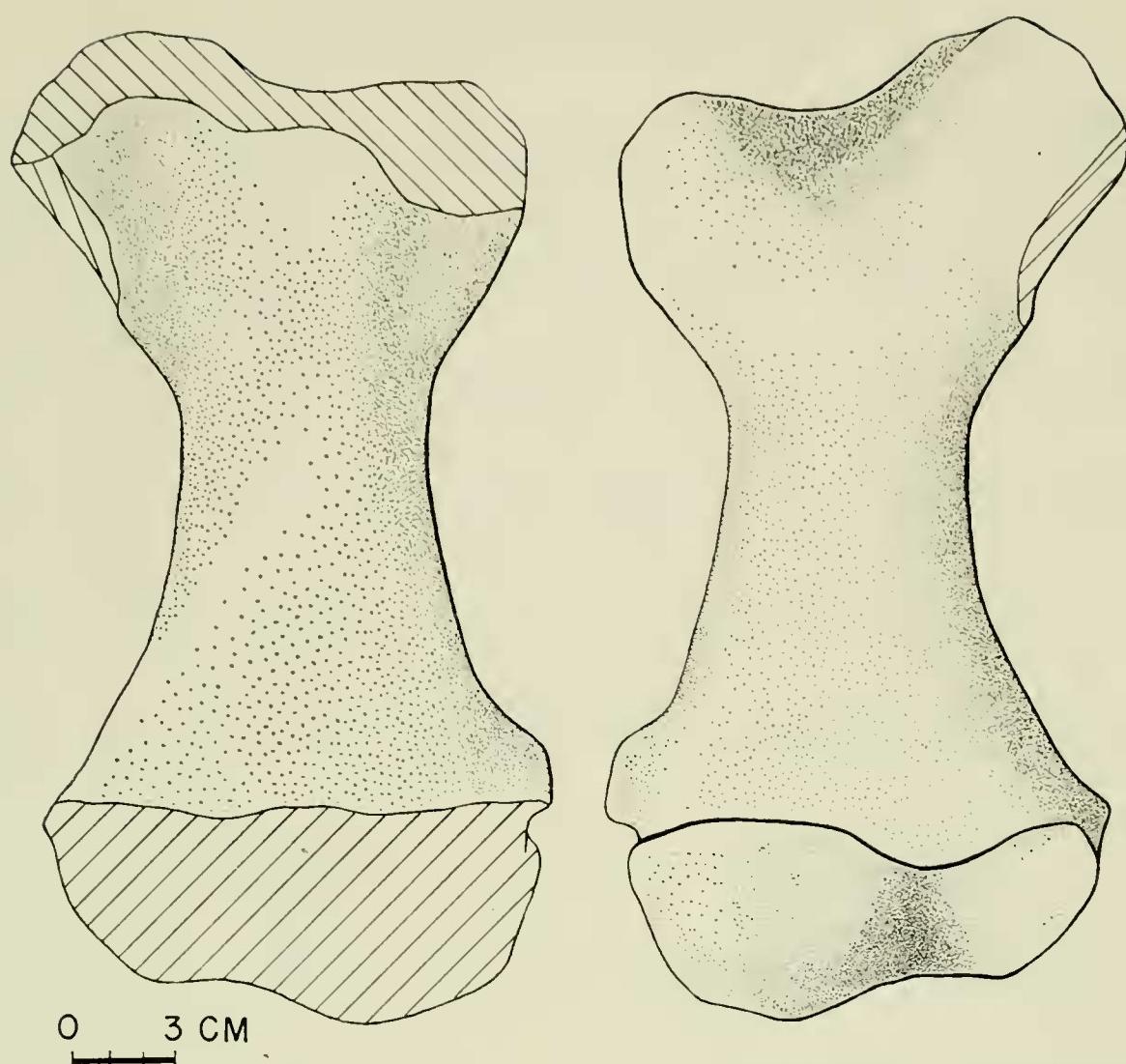
Figure 9. The left femur of *Stupendemys geographicus* (MCNC 244) in dorsal (left) and ventral (right) views.

ACKNOWLEDGMENTS

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